A Revision of Generic Concepts in the Biosystematics of Hawaiian Drosophilidae[1,2,3]

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INTRODUCTION

The genus *Drosophila* was first described by Fallen in 1823, but it was A.H. Sturtevant (1939) who discussed in detail the taxonomic methodology in analyzing and selecting characters which are important in showing phylogenetic relationships between species. Sturtevant (1939), in realization of the problems in the systematics of *Drosophila* species, stated that "...it is desirable that there be available a satisfactory arrangement of species into some scheme of classification that can be taken as indicating their degree of genetic relationships." He carefully selected 33 "good" characters each of which had to be shared by at least two species, and recorded the states of these characters in each of the species he studied. Then by calculating the discordance between each pair of species and deriving a matrix of species pairs, he was able to formulate a classification of the species which was indicative of their phylogenetic relationships. In a sense, Sturtevant's "...description of methods reads like a page from numerical taxonomy" (Throckmorton, 1968). Thus for all practical purposes, modern taxonomic methods (gamma taxonomy) were applied to the classification of the genus *Drosophila* more than 30 years ago and Sturtevant's description of taxonomic methodology has remained a most important contribution to the taxonomy of *Drosophila*.

The endemic Hawaiian drosophilids have undoubtedly undergone explosive evolutionary radiation in a geologically short period of time. Currently, this group of insects is comprised of approximately 500 described species (the endemic fauna may ultimately total more than 800 species) previously divided into eight genera. There are several lines of evidence, however, which show that the present taxonomic status of the Hawaiian drosophilids may give a misleading interpretation of the phylogenetic relationship between species groups. Throckmorton (1966), based on a comparative study of internal anatomy, stated that there are only two major lineages in the evolution of Hawaiian Drosophilidae: The "Drosophiloids" and the "Scaptoids" (the terminology used by Hardy in Carson *et al.*, 1970, "drosophiloid" and "scaptomyzoid" has been adopted in this paper). Corroborating observations

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on the mating behavior patterns by Spieth (1966) showed that there are two basic behavior patterns in the Hawaiian drosophilids; a very elaborate species-specific courtship in the drosophiloids and a simple "assault" courtship in the scaptomyzoids. Based on observations of the metaphase karyotypes, Clayton (1968) summarized that the endemic species of Hawaiian Drosophilidae fall into two chromosomal groups which correspond with the genus *Scaptomyza* and the genus *Drosophila*. Carson *et al.* (1967) judged the "genus" *Idiomyia* to be cogeneric with the genus *Drosophila*, based on the banding patterns of the polytene chromosomes from the salivary gland cells of the third-instar larvae. Yoon *et al.* (1972), also based on an analysis of the banding patterns of polytene chromosomes, showed that there is a high degree of chromosomal homology between the genus *Drosophila* and the endemic genus *Antopocerus* and concluded that these two genera in Hawaii have a common ancestor.

Kaneshiro (1969a) showed that speciation in the picture-winged species of Hawaiian *Drosophila* has resulted in tremendous morphological diversity, but with remarkable stability of the male genitalic structures. Since the classical paper of Sturtevant (1919) in which he showed that the most striking difference between *melanogaster* and the closely related species, *simulans*, was in the structures of the male genitalia, most *Drosophila* taxonomists (e.g. Hsu, 1949; Okada, 1955; and Takada, 1965, 1966) have used male genitalic characteristics to separate closely related species; i.e., species which cannot be easily separated on the basis of external morphological characteristics. However, with the Hawaiian *Drosophila*, there is a high degree of structural similarity in the male genitalia (especially the phallic organs) and for the most part, genitalia cannot be used to differentiate between species within a species subgroup. Kaneshiro (1969a), however, was able to use the genitalic apparatus as a tool for showing phylogenetic relationships of species within the picture-winged species group. His data correlate very closely with data presented by Carson, 1971; Carson *et al.*, 1970; and Clayton *et al.*, 1972 which were based on chromosomal relationships.

In this paper an attempt is made to show that conventional morphological characters, which are used by many Diptera taxonomists, could give a misleading impression of evolutionary divergence in Hawaiian Drosophilidae. It is shown that one must determine what structures are secondary sexual characteristics of males, which are used in the elaborate courtship behavior patterns of the Hawaiian drosophiloids, before selecting various taxonomic characters for the evaluation of major groupings. Based on Kaneshiro's (1969a) findings, a comparative study of the male genitalic structures is shown to be a most important tool in showing phylogenetic relationships in the endemic drosophilid fauna. Drosophiloid species previously placed in five separate genera (including *Idiomyia*) are shown to be only species groups of the genus *Drosophila*. The "key" characters used to differentiate these groups into separate genera do not appear to warrant even the maintenance of subgeneric groupings. Thus, the endemic genera *Antopocerus, Nudidrosophila* and *Ateledrosophila* are sunk as synonyms of *Drosophila* (*Drosophila*).

Materials and Methods

Most of the specimens were obtained from the collection of the Department of Entomology of the University of Hawaii. In a few species the male genitalic structures of six or more specimens were examined to study the

degree of intraspecific variability which may exist. For many species, however, only a few and sometimes only a single specimen was available for such study. It was later found that the intraspecific variability in the shape of the phallic structures was of little importance, and therefore the examination of only a few or even single specimens of a given species was sufficient for the scope of this study. The species studied are listed on Table 1, according to their previously accepted generic groupings. The species previously described in *Antopocerus, Nudidrosophila* and *Ateledrosophila* are listed in Table 2 in the generic grouping now being proposed.

The procedure used in preparing the genitalic materials is the same as that outlined by Kaneshiro (1969a) and will not be repeated here.

TABLE 1. *Previous Taxonomic Arrangements of Species Studied*

Species	*Figure*
Modified-Tarsi Species Group (*Drosophila*)	
Bristle-tarsi subgroup	
D. basimacula Hardy	4A
D. quasiexpansa Hardy	4B
D. perissopoda Hardy	4C
D. expansa Hardy	4D
D. apodasta Hardy	4E
D. seclusa Hardy	4F
D. redunca Hardy	4G
D. (Trichotobregma) petalopeza Hardy	4H
Spoon-tarsi subgroup	
D. mimiconformis Hardy	5A
D. sordidapex Grimshaw	5B
D. incognita Hardy	5C
D. conformis Hardy	5D
D. disticha Hardy	5E
D. dasycnemia Hardy	5F
D. septuosa Hardy	5G
D. neutralis Hardy	5H
Split-tarsi subgroup	
D. pectinitarsus Hardy	6A
D. cnecopleura Hardy	6B
D. propiofacies Hardy	6C
D. cracens Hardy	6D
D. fundita Hardy	6E
D. variabilis Hardy	6F
D. clavata Hardy	6G
D. attenuata Hardy	6H
Antopocerus Species Group	
A. villosus Hardy	7A
A. aduncus Hardy	7B
A. cognatus (Grimshaw)	7C
A. diamphidiopodus Hardy	7D
A. entrichonemus Hardy	7E
A. longiseta (Grimshaw)	7F
A. tanythrix Hardy	7G
A. orthopterus Hardy	7H

TABLE 1. *Previous Taxonomic Arrangement of Species Studied* (Continued)

Species	*Figure*
Nudidrosophila Species Group	
N. lepidobregma Hardy	8A
N. aenicta Hardy	8B
N. eximia Hardy	8C
N. amita Hardy	8D
N. gemmula Hardy	8E
Nudidrosophila Species Group (Continued)	
N. new species A	8F
N. (?) *new species* B	8G
N. (?) *new species* C	8H
D. hirtitibia subgroup	
D. hirtitibia Hardy	9A
D. new species near *hirtitibia*	9B
D. velata subgroup	
D. velata Hardy	9C
D. new species near *velata*	9D
Ateledrosophila Species Group	
A. diamphidia Hardy	10A
A. preapicula Hardy	10B
"Idiomyia" Species Group (*planitibia* subgroup)	
D. planitibia (Hardy)	11A
D. heteroneura (Perkins)	11B
D. silvestris (Perkins)	11C
D. nigribasis Hardy	11D
D. hanaulae Hardy	11E
D. cyrtoloma Hardy	11F
D. ingens Hardy and Kaneshiro	11G
D. melanocephala (Hardy)	11H
D. neoperkinsi Hardy and Kaneshiro	12E
D. obscuripes (Grimshaw)	12F
Miscellaneous Picture-Winged Species	
D. vesciseta Hardy and Kaneshiro	10C
D. hexachaetae Hardy	10D
D. adiastola Hardy	12A
D. spectabilis Hardy	12B
D. picticornis Grimshaw	12G
D. setosifrons Hardy and Kaneshiro	12H

OBSERVATIONS

The details of the major characteristics of male genitalic structures of the major species groups and genera of the drosophiloid group are described below. Major emphasis is placed on species groups in the genus *Drosophila* which show obvious relationships to species in the three previously accepted endemic genera, *Antopocerus, Ateledrosophila, Nudidrosophila* and what was formerly the genus, *Idiomyia*. Figure 1 is a diagrammatic sketch of the external male genitalia of a typical *Drosophila* species. Figure 2 illustrates the male genitalia of a representative species (where possible, the type species was used) of each of the four drosophiloid genera.

TABLE 2. *Proposed Generic Changes*

ANTOPOCERUS GROUP
Drosophila (*Drosophila*) *adunca* (Hardy), **New Comb.**
Antopocerus aduncus Hardy, 1965:44-46.
Drosophila (*Drosophila*) *arcuata* (Hardy), **New Comb.**
Antopocerus arcuatus Hardy, 1965:47-48.
Drosophila (*Drosophila*) *cognata* Grimshaw, 1901, Fauna Hawaiiensis 3(1):69.
Antopocerus cognatus (Grimshaw) Hardy, 1965:48-50.
Drosophila (*Drosophila*) *diamphidiopoda* (Hardy), **New Comb.**
Antopocerus diamphidiopodus Hardy, 1965:50-52.
Drosophila (*Drosophila*) *entrichocnema* (Hardy), **New Comb.**
Antopocerus entrichocnemus Hardy, 1965:52-53.
Drosophila (*Drosophila*) *longiseta* Grimshaw, 1901, Fauna Hawaiiensis 3(1):68.
Antopocerus longiseta (Grimshaw) Hardy, 1965:54-56.
Drosophila (*Drosophila*) *orthoptera* (Hardy), **New Comb.**
Antopocerus orthopterus Hardy, 1965:56-58.
Drosophila (*Drosophila*) *tanythrix* (Hardy), **New Comb.**
Antopocerus tanythrix Hardy, 1965:58-61.
Drosophila (*Drosophila*) *villosa* (Hardy), **New Comb.**
Antopocerus villosus Hardy, 1965:61-62.

ATELEDROSOPHILA GROUP
Drosophila (*Drosophila*) *diamphidia* (Hardy), **New Comb.**
Ateledrosophila diamphidia Hardy, 1965:63-64.
Drosophila (*Drosophila*) *preapicula* (Hardy), **New Comb.**
Ateledrosophila preapicula Hardy, 1965:64-66.

NUDIDROSOPHILA GROUP
Drosophila (*Drosophila*) *aenicta* (Hardy), **New Comb.**
Nudidrosophila aenicta Hardy, 1966:227-231.
Drosophila (*Drosophila*) *amita* (Hardy), **New Comb.**
Nudidrosophila amita Hardy, 1965:565-567.
Drosophila (*Drosophila*) *eximia* (Hardy), **New Comb.**
Nudidrosophila eximia Hardy, 1965:567-569.
Drosophila (*Drosophila*) *gemmula* (Hardy), **New Comb.**
Nudidrosophila gemmula Hardy, 1965:569-571.
Drosophila (*Drosophila*) *lepidobregma* (Hardy), **New Comb.**
Nudidrosophila lepidobregma Hardy, 1965:571-573.

The Modified-Tarsi Species Group

This group of *Drosophila* species is comprised of three subgroups, namely the "bristle-tarsi," "spoon-tarsi," and "split-tarsi" (Throckmorton, 1966) which are characterized by males having modifications of the tarsal segments of the forelegs. Males of the bristle-tarsi group have a clump of heavy bristles at the dorso-apical end of the front basitarsus, as in *basimacula* Hardy (see Figure 42a, Hardy 1965:268) and *expansa* Hardy (see Figure 91a, Hardy 1965:268). There are 10 described species in this subgroup. The spoon-tarsi species are characterized by males having the second tarsal segment of the forelegs modified into a short, flattened, concave segment as in *disticha* Hardy (see Figure 82a, Hardy 1965:250) and *dasycnemia* Hardy (see Figure 74a, Hardy 1965:237). There are 10 described species in this subgroup. Males of the split-tarsi group have a peculiar appendage arising near the apex

of the basitarsus of the forelegs. Furthermore, the tarsi of the forelegs consist of only four segments in contrast to the normal five tarsal segments found in other drosophilids. Examples of split-tarsi species are *cracens* Hardy (see figure 69a, Hardy 1965:227) and *pectinitarsus* Hardy (see Figure 161 c and d, Hardy 1965:406). There are 14 described species in the split-tarsi subgroup. The females of these modified tarsi subgroups lack any of the peculiar development of the foretarsi.

The aedeagus of all the species in this group is characterized by a small rounded, preapical protuberance. Also in most of the species there is a second small "hump" just basad to the preapical protuberance (Figures 4, 5, 6). Although the genitalia of most of the species in these three subgroups were studied, the aedeagi of only a representative number of species are illustrated. For the most part, the aedeagi which are most different and considered to be most representative of each of the subgroups are illustrated.

Another species, *D. petalopeza,* which was described in a separate subgenus, *Trichotobregma* Hardy (1965), is here placed in the bristle-tarsus group. This species is characterized by the peculiar development of the head bristles. It differs from typical *Drosophila* by lacking the proclinate and anterior reclinate bristles and by having numerous long, hair-like bristles on the antero-lateral margins of the front. Also, there is a tuft of long hairs on the ocellar triangle in addition to a pair of tiny ocellar bristles (see Figure 221a in Hardy, 1965:533). The females apparently also lack the proclinate bristles, but the two reclinate bristles are distinguishable from a series of four to six short bristle-like hairs on the orbits between the anterior and posterior reclinates. The pair of ocellar bristles are normal (conspicuously large) in development. On the basis of the peculiar chaetotaxy of the head of *petalopeza,* Hardy felt it necessary to place this species in a separate subgenus. Nevertheless, the basitarsus of the forelegs of *petalopeza* males has a peculiar bristle arrangement which is similar to the basitarsus of some of the bristle-tarsi species. The aedeagus is also characteristic of the modified tarsi group and is therefore illustrated (Figure 4H) with that of some of the bristle-tarsi species.

The Antopocerus Species

The genus *Antopocerus* Hardy consists of nine described species and is characterized by the males having large, porrect first antennal segments (Figure 3A). Also, the arista is long and whip-like, densely covered with short hairs on the dorsal surface, and bare on the ventral surface except for some short preapical hairs in some species (see also Figures 7a, 8a, 10b, in Hardy, 1965). The front legs of the males typically have long ciliation on both tibia and tarsus (see Figures 10c, 11a and 14c in Hardy, 1965). Note that in several of the species, the second tarsomere of the front legs is very short; only a fraction of the length of the basitarsus (e.g. *arcuatus,* Figure 8d in Hardy, 1965:47; *diamphidiopodus,* Figure 10c in Hardy, 1965:51; *orthopterus,* Figure 13a in Hardy, 1965:57; and *tanythrix,* Figure 14c in Hardy, 1965:59). The females in this group, on the other hand, lack the enlarged first antennal segment and have a typical *Drosophila* arista with the usual long aristal rays. Also, the front legs of females lack the various ornamentations found in the males.

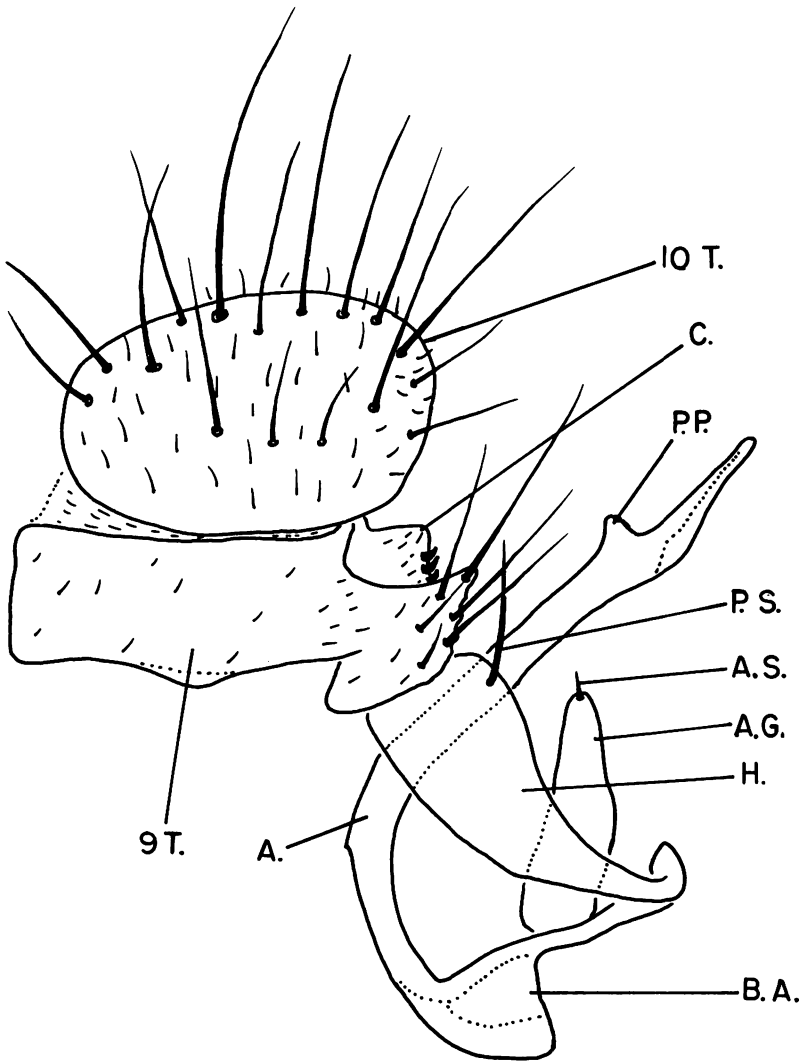

FIG. 1. Diagrammatic sketch of external male genitalia. A. aedeagus, A.G. anterior gonapophysis (paramere), A.S. apical sensilum, B.A. basal apodeme of aedeagus, C. clasper, H. hypandrium, P.P. preapical protuberance of aedeagus, P.S. paramedian spine, 9T. ninth tergum, 10T. tenth tergum (anal plate).

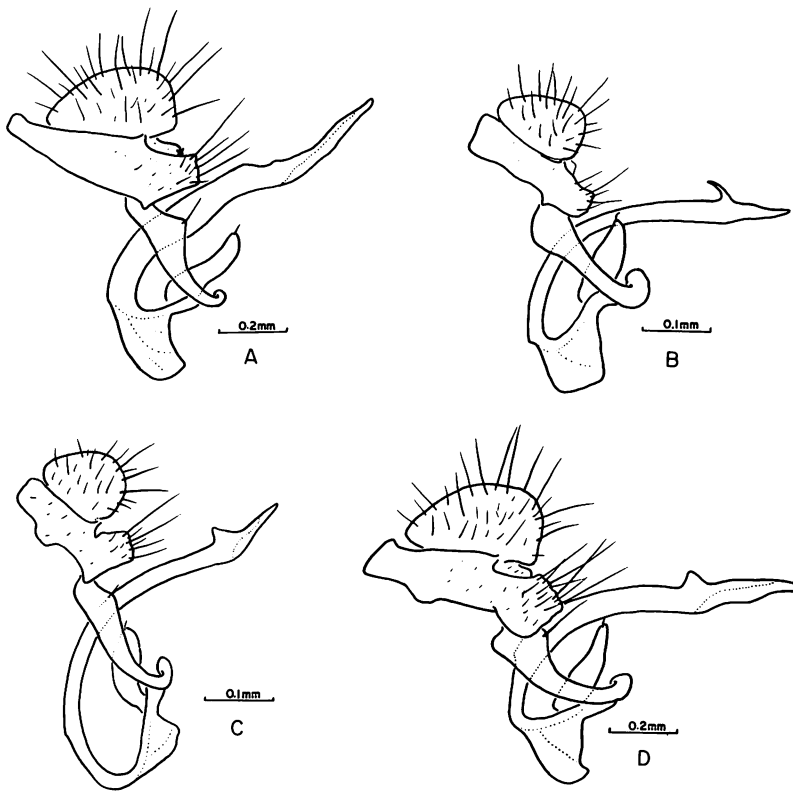

FIG. 2. Lateral view of external male genitalia of: A, *Antopocerus longiseta*; B, *Nudidrosophila lepidobregma*; C, *Ateledrosophila diamphidia*; D, *Idiomyia neoperkinsi*.

The phallic structures, especially the overall shape of the aedeagus, resemble those of the modified-tarsi species described above. The aedeagus characteristically has a small preapical protuberance and a prominent second "hump" just basad to the preapical protuberance as shown in Figure 7. The aedeagi of all of the described *Antopocerus* species except *arcuatus* (specimens not readily available) were studied and illustrated.

The Nudidrosophila Species

The genus *Nudidrosophila* Hardy consists of five described species and is characterized by the males lacking the normal orbital and ocellar bristles and having microscopic pubescense or setae on the front (Figure 3B and Figure 14a in Hardy 1966:228). The females, however, lack the peculiar development on the head of the males (see Figure 14b in Hardy 1966:228) and are not readily distinguishable from females of *Drosophila* species.

The shape of the preapical protuberance of the aedeagus is very characteristic in *Nudidrosophila* species. It is long and recurved and forms a hook-like structure near the apical end of the aedeagus as shown in Figure 8.

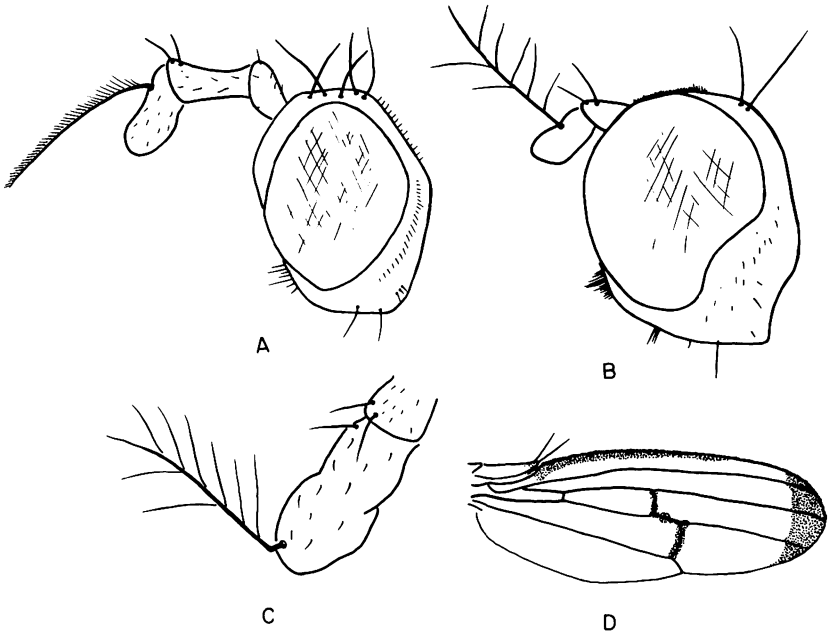

FIG. 3. Drawings showing "key" characters used to separate species into genera. A, head of male *Antopocerus* species showing porrect antenna; B, head of male *Nudidrosophila* species showing lack of orbital bristles and presence of microscopic pubescence on frons; C, preapical position of arista on antenna of *Ateledrosophila* species; D, wing of "*Idiomyia*" species with extra crossvein in cell R5.

Three undescribed species which are believed to belong to this group were also studied. One definitely fits Hardy's (1965) concept of *Nudidrosophila,* but is distinctly different from any of the five described species. The aedeagus is also characteristic of the other *Nudidrosophila* species (Figure 8F). The other two species, however, are peculiar in that the posterior reclinate, proclinate and ocellar bristles are well developed. The middle orbital or anterior reclinate bristle cannot be differentiated from a patch of long hairs on the frons. Nevertheless, the aedeagi (Figures 8G and 8H) are very similar to those of *Nudidrosophila,* and these two species are therefore being placed in this group.

The hirtitibia and velata subgroups

The *hirtitibia* subgroup consists of only one described species from Oahu (*D. hirtitibia*), and at least one undescribed species from the island of Hawaii. There are two other species which appear to belong in this subgroup, but only a few specimens of each of these are available. They are extremely close to *hirtitibia* and therefore the description of these will be deferred until larger samples can be collected and studied.

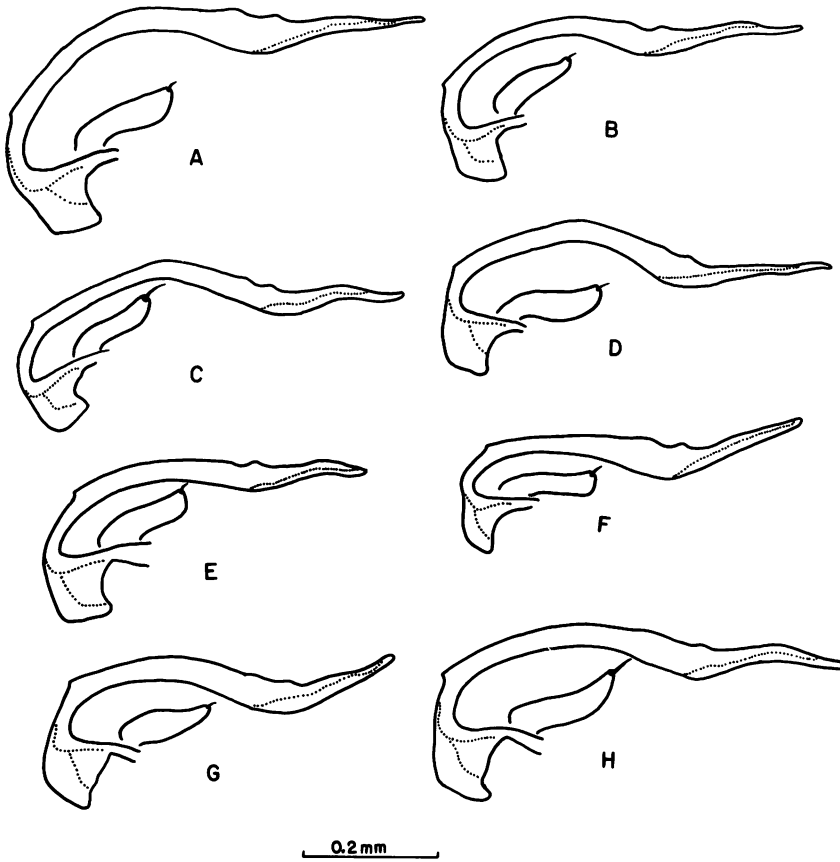

FIG. 4. Phallic organs of the bristle-tarsi subgroup; A, *basimacula*; B, *quasiexpansa*; C, *perissopoda*; D, *expansa*; E, *apodasta*; F, *seclusa*; G, *redunca*; H, (*Trichotobregma*) *petalopeza*.

The *hirtitibia* subgroup is characterized by having head bristles typical of *Drosophila* species except that the anterior reclinate bristle is long and hair-like; longer than both the proclinate and posterior reclinate bristles. The species in this subgroup also have long ciliation on both the tibiae and tarsi of the front legs (see Figure 112b in Hardy, 1965:307).

The *velata* subgroup also consists of only one described species from Oahu (*D. velata*) and at least one undescribed species from Kauai. These two species are characterized by having the normal head bristles found in *Drosophila,* and by having curled cilia on the front tarsi (see Figure 205c in Hardy, 1965:498). The front tibiae lack long ciliation.

The aedeagus of the species in both the *hirtitibia* and *velata* subgroups are very characteristic and strongly resemble those of *Nudidrosophila* species. The preapical protuberance is shaped into a hook-like structure as shown in Figures 9A through 9D.

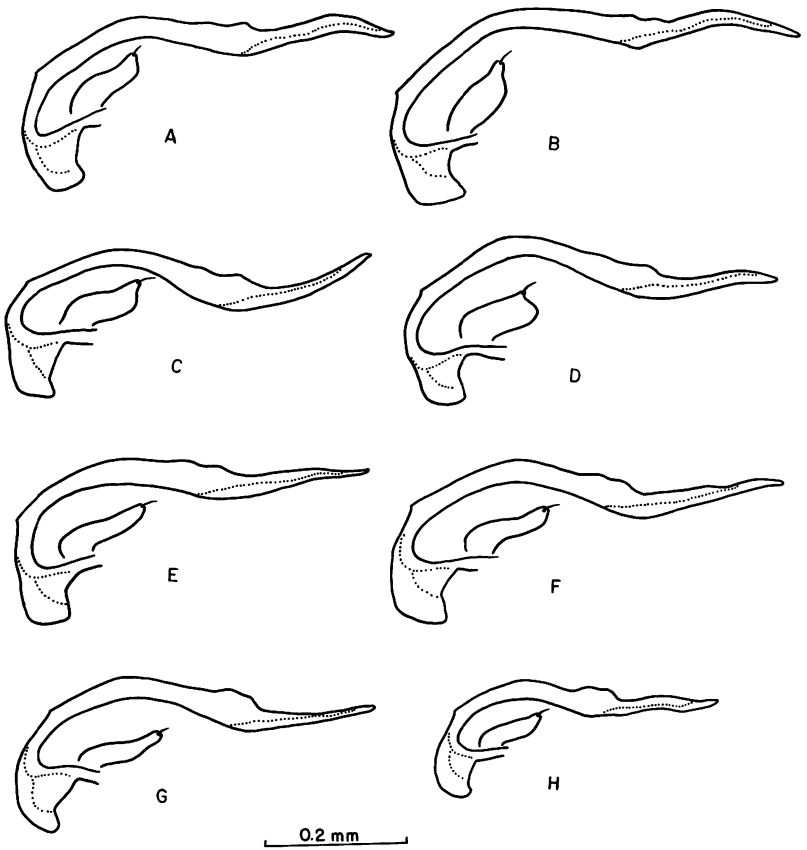

FIG. 5. Phallic organs of the spoon-tarsi subgroup: A, *mimiconformis*; B, *sordidapex*; C, *incognita*; D, *conformis*; E, *disticha*; F, *dasycnemia*; G, *septuosa*; H, *neutralis*.

The Ateledrosophila Species

The genus *Ateledrosophila* Hardy consists of two described species and is readily differentiated from other Hawaiian drosophilids by the preapical arista (Figure 3C and also 16a and 17a in Hardy, 1965:64-65) and the lack of anterior reclinate and ocellar bristles. Also, the front is conspicuously setose and in this respect very much resemble the head of *Nudidrosophila* species. However, the aedeagus lacks the hook-like preapical protuberance and is otherwise readily differentiable from that of *Nudidrosophila* species (Figure 10).

The "Idiomyia" Species

The species of this group were placed in a separate genus on the basis of the presence of an extra crossvein in cell R5 in the wings of both sexes (Figure 3D). All of the species have distinctive wing maculations, and some of them are probably the largest known drosophilids in the world, with a wing span of about 20mm or more (Hardy, 1969).

Seventeen described species have been assigned to this group. Kaneshiro (1969a) showed that two species, *neogrimshawi* and *clavisetae,* which fit the concept of the "genus" *Idiomyia,* (Grimshaw, 1901), are actually closely related to the *adiastola* subgroup on the basis of the shapes of the aedeagi (see Figure 2 in Kaneshiro, 1969a:57; also compare Figure 12A and B with 12C and D). The aedeagi of the remaining 13 species in this group are characterized by being relatively broad and short in relation to the basal apodeme, and by a prominent, rounded preapical protuberance (Figure 11).

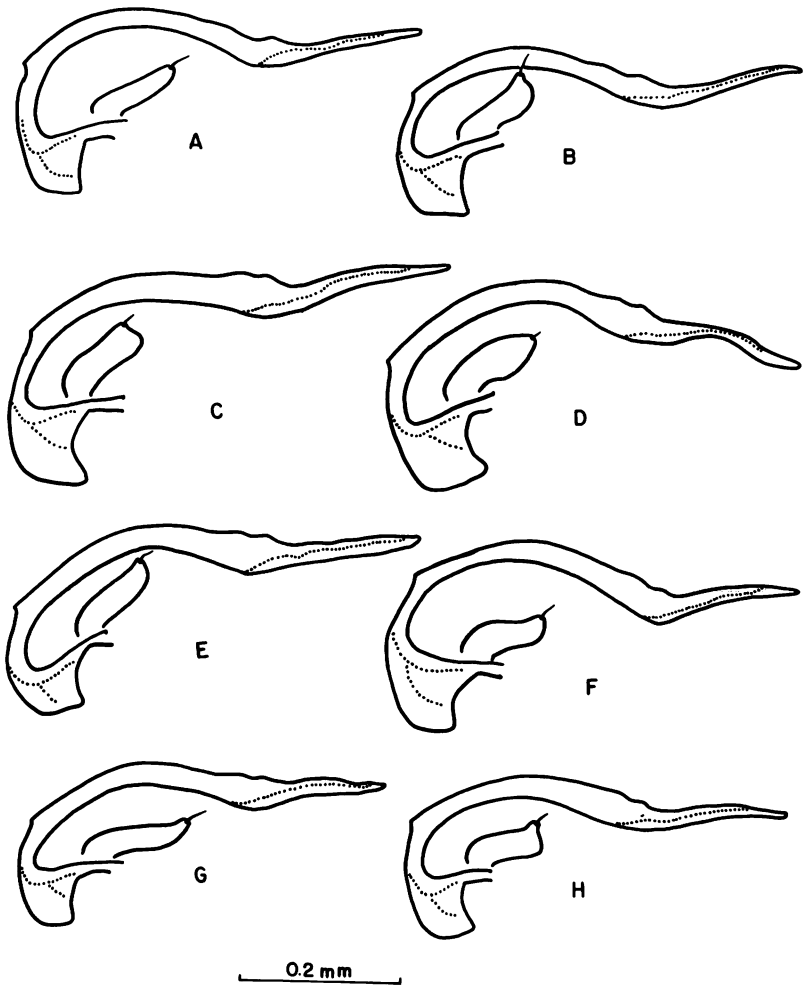

FIG. 6. Phallic organs of the split-tarsi subgroup: A, *pectinitarsus*; B, *cnecopleura*; C, *propropiofacies;* D, *cracens;* E, *fundita;* F, *variabilis;* G, *clavata;* H, *attenuata.*

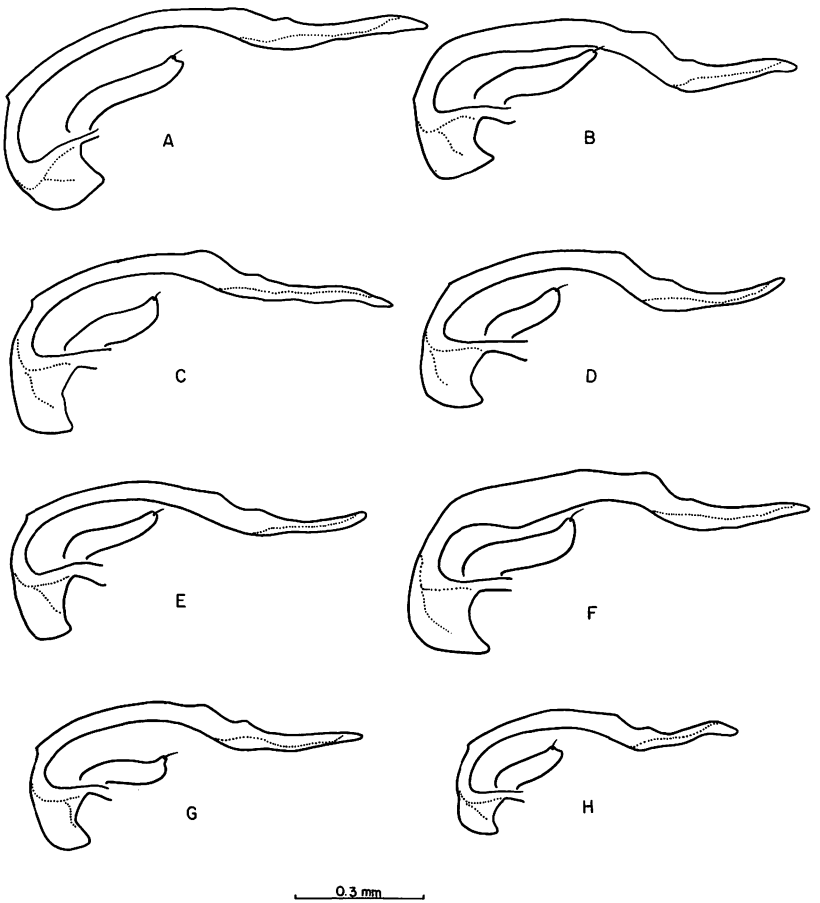

FIG. 7. Phallic organs of the *Antopocerus* species: A, *villosus*; B, *aduncus*; C, *cognatus*; D, *diamphidiopodus*; E, *entrichocnemus*; F, *longiseta*; G, *tanythrix*; H, *orthopterus*.

Miscellaneous Picture-Winged Species

The aedeagus of a few picture-winged species are discussed and illustrated as supporting evidence for some of the concepts presented in this paper. Those of *vesciseta* and *hexachaetae* are illustrated in Figures 10C and D while those of *adiastola, spectabilis, setosifrons* and *picticornis* are illustrated in Figure 12.

DISCUSSION

Throckmorton's (1966) comparative study of the internal anatomy of representative species from all of the major groups of Hawaiian drosophiloids showed that the endemic fauna is comprised of only two lineages (the drosophiloids and the scaptomyzoids) which probably evolved from a single

ancestral founder population. This remarkable finding was totally unexpected because of the tremendous differentiation in the external morphology of the drosophiloid species. These bizarre morphological characters, which are secondary sexual structures usually found only in males, were used as key differentiating characters between species groups, and led earlier taxonomists to designate as genera or subgenera those groups of species which shared these various "key" characters. Throckmorton's study revealed that despite the tremendous morphological diversity, the endemic drosophiloids represent an extremely close knit group of species, and that most of these variations in external morphology are phylogenetically superficial.

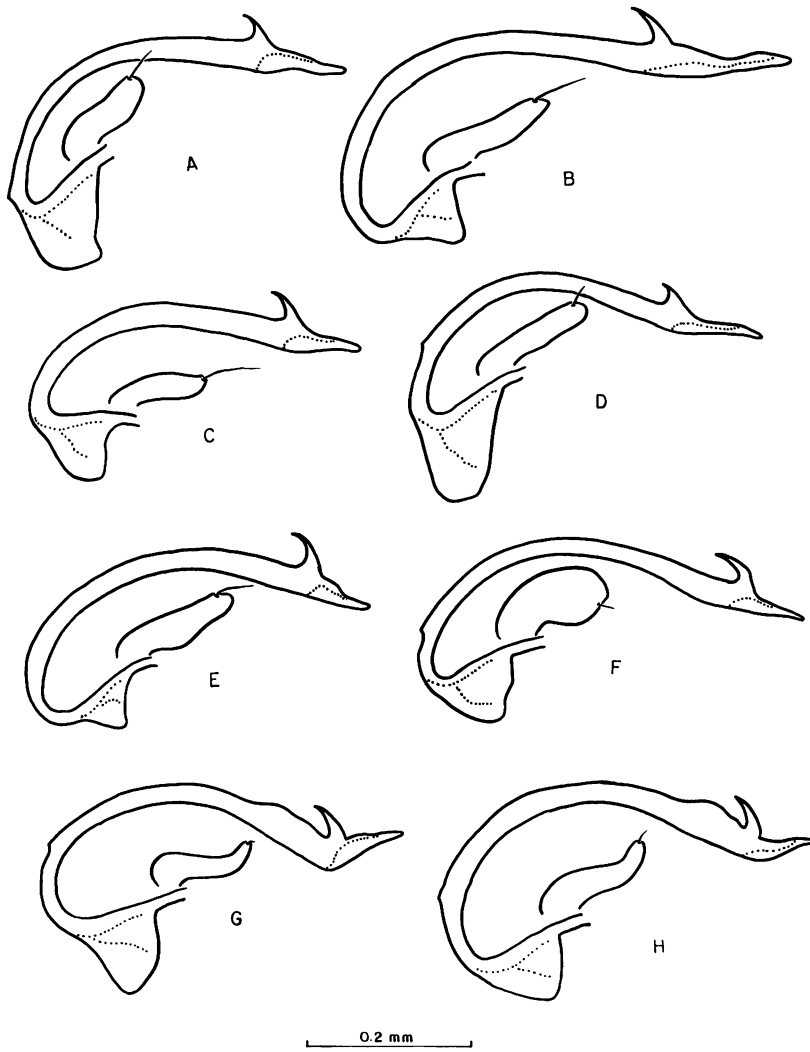

FIG. 8. Phallic organs of the *Nudidrosophila* species: A, *lepidobregma*; B, *aenicta*; C, *eximia*; D, *amita*; E, *gemmula*; F, *new species* A; G, *new species* B; H, *new species* C.

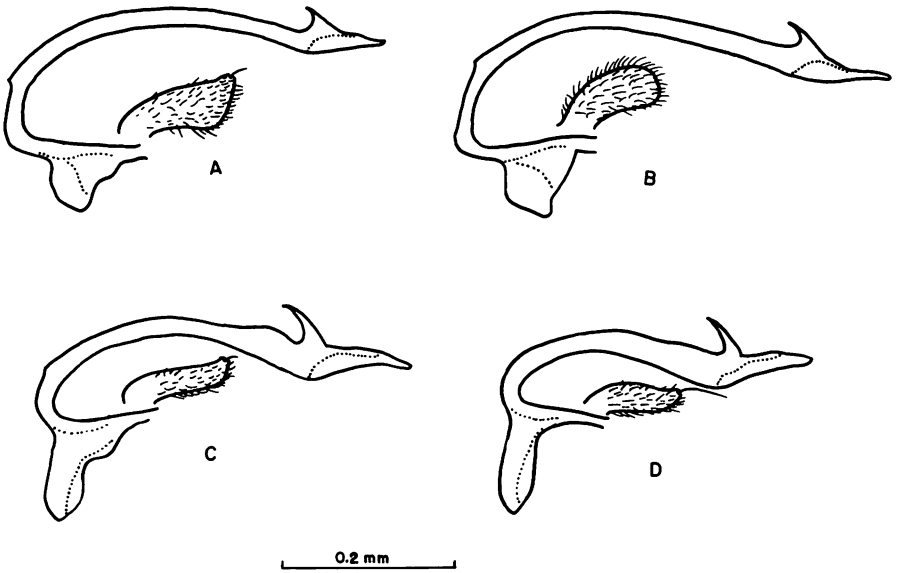

FIG. 9. Phallic organs of *D. hirtitibia* subgroup: A, *hirtitibia*; B, *new species* close to *hirtitibia*. Phallic organs of *D. velata* subgroup; C, *velata*; D, *new species* close to *velata*.

A preliminary investigation of the external male genitalic structures of representative species of all of the major species groups and the eight genera, showed that there are two primary types of genitalic structures in the Hawaiian drosophilids. the first type, for the most part, is characterized by a relatively simple aedeagus, clasper, and hypandrium, as observed by Kaneshiro (1969a) in the picture-winged species group. This type is found in the genera *Drosophila* (except for the subgenus *Engiscaptomyza* Kaneshiro, 1969b), *Antopocerus, Nudidrosophila, Ateledrosophila,* and what was formerly the genus *Idiomyia* (Figure 2A-D respectively). These four groups will be referred to as the "drosophiloids." The second type of genitalic apparatus is found in the genera *Celidosoma, Grimshawomyia, Titanochaeta* and *Scaptomyza* and the subgenus *Engiscaptomyza* in the genus *Drosophila* (these will be referred to as the "scaptomyzoids") and is characterized by a complex genitalic apparatus. In the drosophiloids, the simple genitalic structure is in contrast to the tremendous diversity in external morphological structures such as wing markings, ornamentations of the forelegs, modifications of the labella, etc. In contrast, the scaptomyzoids have complex genitalic structures but have external morphological characters which are very similar and therefore not reliable in differentiating between closely related species. Hardy (1965) found that comparisons of the male genitalic structures were not necessary to distinguish between the drosophiloid species, but that for the most part, a comparative study of the male genitalic structures was the only way to distinguish between closely related scaptomyzoid species.

Due to the lack of sufficient biological information, (i.e., ecology, behavior, cytology, etc.) on most of the scaptomyzoid species it is rather premature to propose a revision of the generic and subgeneric concepts of this group. Preliminary data from comparisons of internal anatomy (e.g., shape of spermatheca, ventral receptacles, paragonia, vasa deferentia, ejaculatory bulb, malpighian tubules, etc.) indicate that the scaptomyzoid species, at least those currently classified in the genus *Titanochaeta* and the five endemic subgenera of the genus *Scaptomyza,* represent a very close knit group of species (Throckmorton, 1966).

Observations on the courtship behavior patterns of the scaptomyzoids are by no means exhaustive, but nevertheless they indicate a distinctive deviation from those of the drosophiloids. Lek behavior (which is displayed by many of the drosophiloid species groups) is apparently absent, and the courtship and mating behavior patterns are relatively simple in the scaptomyzoids. Therefore, there has not been selection for the development of the elaborate secondary sexual structures as observed in the drosophiloids, and there is an obvious lack of external morphological diversity between closely related species. The scaptomyzoids have instead evolved highly complex genitalia in the males which are useful in differentiating between closely related species. However, until more biological data (especially in regard to the modes of reproductive isolation and speciation) are available for the scaptomyzoid species, the taxonomic status of this group will be left for future analysis.

A comparative study of the courtship and mating behavior patterns of representative species of most of the Hawaiian drosophiloids by Spieth (1966, 1968) showed that most of the extraordinary sexually dimorphic structures

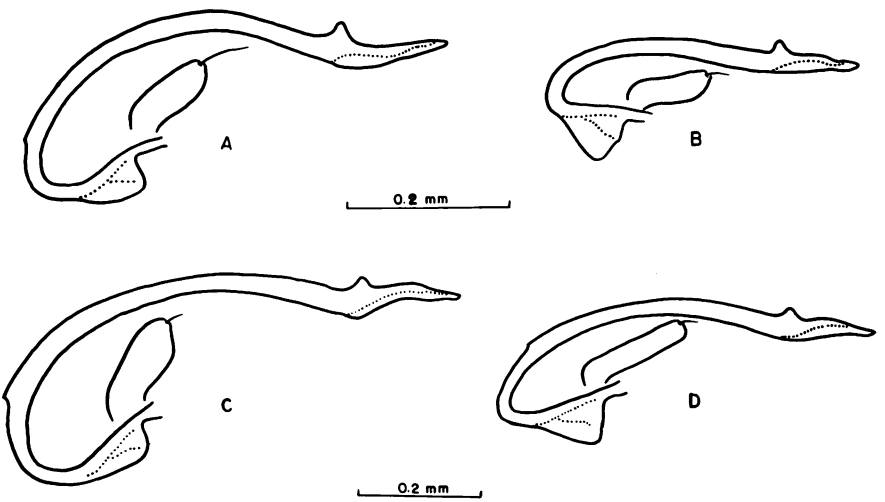

FIG. 10. Phallic organs of *Ateledrosophila* species: A, *diamphidia*; B, *preapicula*. Phallic organs of *Drosophila* species: C, *vesciseta*; D, *hexachaetae*.

found only in the males are utilized in an elaborate, species-specific courtship behavior pattern. These secondary sexual structures are also found in a small percentage of the drosophiloid fauna of the rest of the world; for example, the sex combs in the males of *melanogaster* and *ananassae*. However, these are rare exceptions compared to the frequent occurrence of such dimorphic structures in the males of the Hawaiian species. Spieth (1966, and in Carson *et al.*, 1970) therefore concluded that an elaborate courtship pattern evolved as a highly effective premating isolating mechanism during the speciation of Hawaiian drosophiloids.

It is clear that a careful assessment of the biological factor or factors which may be involved in isolation mechanisms between species is crucial in deciding which character or characters are phylogenetically important and which are not. For instance, in Hawaiian drosophiloid species, since elaborate courtship behavior patterns appear to be one of the major isolating mechanisms between species, the bizarre secondary sexual characters found in the males of the species are not important in showing phylogenetic relationships between species groups. Indeed, species which share similar sexually dimorphic structures (e.g. the species in the bristle-tarsi species group) are phylogenetically closely related. However, it will be shown that the species previously placed in the genus *Antopocerus* also are closely related to the bristle-tarsi species, despite the tremendous differences in morphological characters of the males which separate these two groups. It should be emphasized that females of all of these species groups are typical of the genus *Drosophila*. The ensuing discussion is an explanation of the observed similarities in the phallic structures of representative species of the major drosophiloid groups, which indicate close relationships between groups which are otherwise morphologically very different. It will be shown that the various "key" characters used to differentiate the drosophiloids into the genera *Antopocerus, Nudidrosophila, Ateledrosophila*, and what was formerly the "genus" *Idiomyia*, are not "good" generic characters.

Carson *et al.*, (1967) presented chromosomal evidence which indicate that the genus *Idiomyia* is cogeneric with the genus *Drosophila*. They showed that two of the species, *clavisetae* and *neogrimshawi*, which have an extra crossvein in cell R5, differed from several picture-winged species (i.e., *adiastola* subgroup species) which are typical *Drosophila* species and lack the extra crossvein, by only five fixed chromosomal inversions. The other "*Idiomyia*" species differ from *clavisetae* and *neogrimshawi* by 25+ inversions. The phallic structures of *clavisetae* and *neogrimshawi* (Figures 12C and 12D respectively) are shown to be similar to species in the *adiastola* subgroup (c.f. Figures 12A and 12B) as reported by Kaneshiro (1969a), while the phallic structures of the remaining *Idiomyia* species (e.g. Figures 12E and 12F) are distinctly different and more closely resemble those of *picticornis* and *setosifrons* (Figures 12G and 12H respectively). It is apparent that the extra crossvein in cell R5 arose independently in the two lineages and therefore is not a valid generic character.

Spieth (1966, 1968) observed that the unique development of the antennae in the males of *Antopocerus* species evolved as a structure used in the elaborate courtship behavior pattern. Besides the various other secondary sexual structures found on the forelegs of the males, the species in this

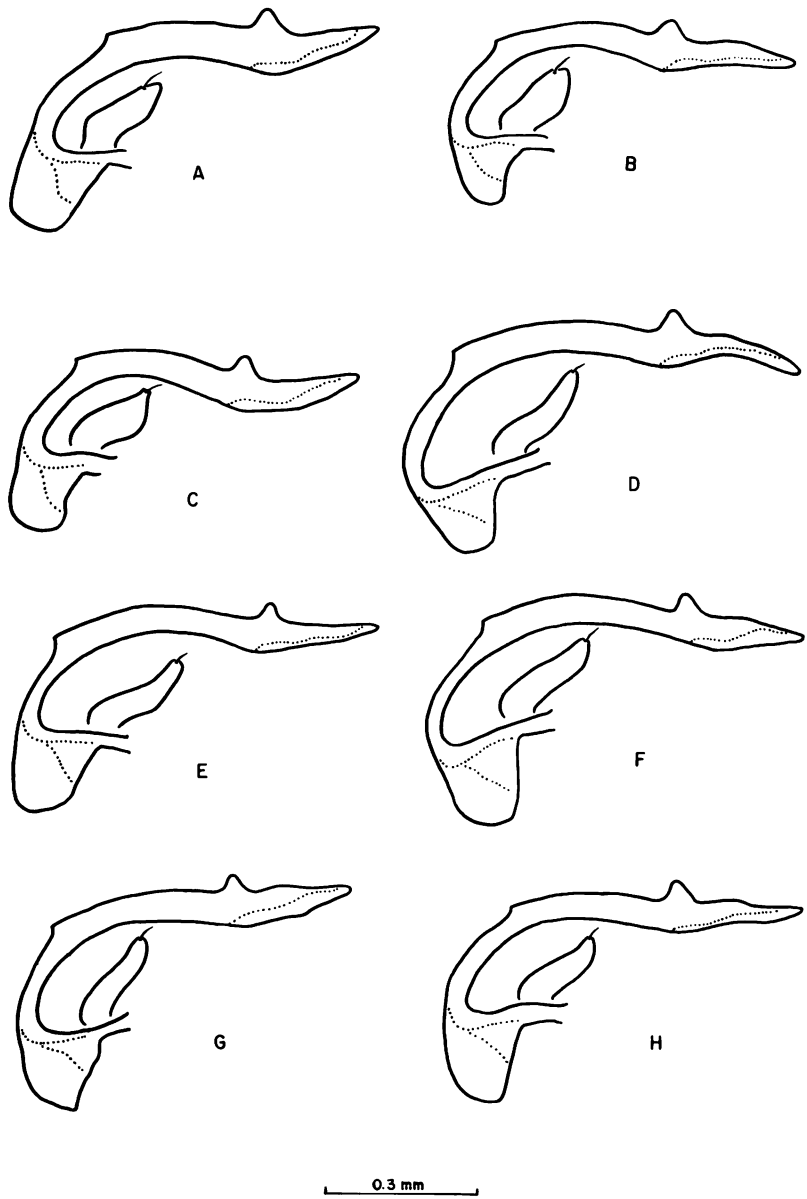

FIG. 11. Phallic organs of "*Idiomyia*" species: A, *planitibia*; B, *heteroneura*; C, *silvestris*; D, *nigribasis*; E, *hanaulae*; F, *cyrtoloma*; G, *ingens*; H, *melanocephala*.

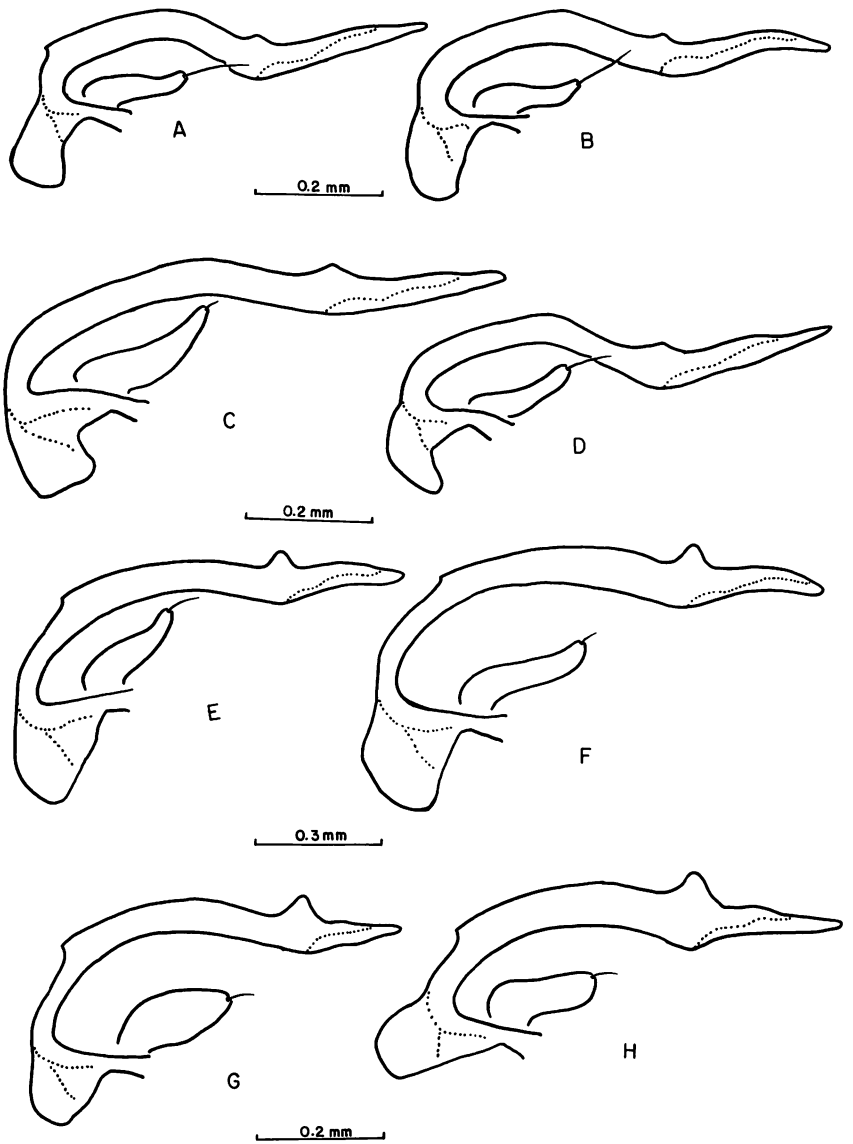

FIG. 12. Phallic organs of: A, *adiastola*; B, *spectabilis*; C, *clavisetae*; D, *neogrimshawi*; E, *neoperkinsi*; F, *obscuripes*; G, *picticornis*; H, *setosifrons*.

genus otherwise fit the characteristics of the genus *Drosophila*. Except for the slightly enlarged first antennal segment, the females of this genus are, for the most part, typical of females of the endemic *Drosophila* species.

Throckmorton (1966), on the basis of internal anatomy, showed that the *Antopocerus* species have characteristics which are mainly shared by the modified-tarsi species groups (i.e. the bristle-tarsi, the spoon-tarsi, and the split-tarsi groups) in the genus *Drosophila*. Heed (1968) reported that the *Antopocerus* species inhabit a very similar ecological niche to that of the modified-tarsi species. He found that all of the *Antopocerus* and modified-tarsi species which he reared from field collected substrates, bred in fermenting leaves of various endemic plants, especially *Cheirondendron* species (Araliaceae). Kambysellis and Heed (1971), in their study of oogenesis and the correlation of ovarian development to ecological habitats in natural populations of Hawaiian drosophiloids, showed that despite their large size, adults of *Antopocerus* species have relatively few ovarioles per ovary and have a similar ovarian development to that of the modified-tarsi species. Yoon *et al.* (1972), based on comparisons of the banding patterns of the polytene chromosomes, showed that *Antopocerus tanythrix* has about 25% of its total genome homologous with that of *D. mimica*, which is an endemic Hawaiian *Drosophila* belonging to a large group of species with modifications of the labellum of the males (the modified-mouthparts species group). Yoon (personal communication) is currently analyzing the polytene chromosomes of several modified-tarsi species and is attempting to homologize the chromosomes of *Antopocerus* species with those of the modified-tarsi species. On the basis of the high degree of chromosomal homology between *A. tanythrix* and *D. mimica*, Yoon *et al.* (1972) concluded that these two genera probably arose from a common ancestor.

At this point, another species, *D. (Trichotobregma) petalopeza*, should be discussed. Indeed, the bizarre development of the chaetotaxy of the head is an extraordinary deviation from typical *Drosophila* characteristics, and would conventionally be a "good" taxonomic character warranting at least a subgeneric ranking. Nevertheless, Spieth (1966), in his observations of the courtship behavior patterns of *petalopeza*, showed that the basitarsus of the forelegs is used in the same manner as observed in the bristle-tarsi species. Heed (1968) reported that, ecologically, the larvae of *petalopeza* occupy the same niche (i.e. fermenting leaves of endemic plants) as do the other modified-tarsi species. Moreover, examination of the male genitalic structures indicated a close relationship to the modified-tarsi species and that *petalopeza* should be included as part of the bristle-tarsi subgroup in the subgenus (*Drosophila*).

On the basis of the evidence presented by Throckmorton (1966), Heed (1968), Kambysellis and Heed (1971), Yoon *et al.* (1971) and the similarities in the genitalic structures, it is clear that the species described in the genus *Antopocerus* are probably only a species group which is very closely related to the modified-tarsi species group in the genus *Drosophila* (Table 2). *Antopocerus* is therefore sunk as a synonym of *Drosophila*.

The endemic genus *Nudidrosophila* Hardy would appear to be a bona fide group of generic rank on the basis of the striking development of the

chaetotaxy of the heads of males. The females, however, are indistinguishable from typical *Drosophila* females. Although Spieth has not made a thorough investigation of the courtship behavior patterns of the *Nudidrosophila* species, it is most probable that these bizarre male characters are secondary sexual structures which are used in courtship behavior. Interestingly, this peculiar development of the head bristles has occurred in two other species in the Hawaiian fauna. Spieth (1966 and personal communication) has studied the courtship behavior of both *D.* (*Trichotobregma*) *petalopeza* (see discussion above) and *D. setosifrons* Hardy and Kaneshiro (a picture-winged species). He found that the peculiarly developed head bristles are used by the males to push against the underside of the female's wings during part of the courtship pattern. It is likely that the head bristles of *Nudidrosophila* species are used in a similar manner in their courtship behavior.

On the basis of the overall similarity of the females of *N. aenicta* and *D. hirtitibia*, and especially the striking resemblance in the development of the ovipositors, Hardy (1966) stated that "...it is evident that *Nudidrosophila* should not be retained as a genus but probably should be sunk as a direct synonym of *Drosophila* even though on the basis of the males there appear to be very striking differences and even though the males characters depart radically from the present concept of *Drosophila*." Although Throckmorton (1966) did not comment on the direct relationship of *N. aenicta* with *D. hirtitibia*, he did conclude that *Nudidrosophila* species have internal structures which are typical drosophiloid characteristics. Re-examination of the figures of some of the internal structures of *N. aenicta* and *D. hirtitibia* showed that there are indeed extremely close similarities in the internal anatomy of these two species.

The aedeagi of the *Nudidrosophila* species are very characteristic in that the preapical protuberance is recurved into a hook-like structure (Figure 8). This would appear to be a key character which would differentiate this group from the rest of the drosophiloids. However, it was found that *D. hirtitibia*, *D. velata*, and two new undescribed species, one closely related to *hirtitibia* and the other close to *velata*, have precisely this same characteristic in the preapical protuberance of the aedeagus.

It is clear that the peculiar head bristles found in *Nudidrosophila* species have evolved as structures used in the elaborate courtship behavior patterns of this group. On the basis of its extremely close relationship to the *D. hirtitibia* group, as shown by Throckmorton's study of the internal anatomy, Hardy's comparisons of the female ovipositors, and especially the similarities in the peculiar shape of the aedeagus, *Nudidrosophila* should not be retained as a separate genus, and is sunk as a synonym of *Drosophila* (Table 2).

Unfortunately, there has been very little work done on the biology of the *Ateledrosophila* group of species. They are rare and only incidentally collected. Throckmorton's (1966) study of the internal anatomy nevertheless shows that the species previously placed in this endemic group have some structures which are of typical drosophiloid characteristics. The general shape of the aedeagus also indicates that this group is obviously close to the drosophiloids.

On the basis of the peculiar chaetotaxy of the head, *Ateledrosophila* species would appear to be closely related to *Nudidrosophila*. However, the

former lack the hook-like appearance of the preapical protuberance of the aedeagus which is so characteristic of the *Nudidrosophila* group. Rather, the aedeagus in the *Ateledrosophila* group is slender and elongate with a small, rounded preapical protuberance which closely resembles those of some of the picture-winged *Drosophila* species (e.g. *vesciseta* and *hexachaetae* as in Figures 10C and 10D respectively). As with the species previously placed in the genera *Antopocerus* and *Nudidrosophila*, the females of *Ateledrosophila* are indistinguishable from females of *Drosophila* species. This is again an indication that the "key" male characteristics used to differentiate these species into separate genera are structures adapted for use in the elaborate courtship behavior patterns which apparently play an important role as reproductive barriers between the drosophiloid species. These bizarre morphological variants (from typical *Drosophila* characteristics) are therefore not valid as key generic characters. On this basis, the genus *Ateledrosophila* also is sunk as a junior synonym of *Drosophila* (Table 2).

Summary and Conclusion

Sturtevant observed that a classification of species should be presented in a scheme which indicates phylogenetic relationships between species and species groups. He proposed that such a classification be based on "an aggregate of characters" which can be analyzed and "weighted" in terms of their phylogenetic significance in the evolution of the group. In other words, characters which are important in showing phylogenetic relationships between species or species groups, should outweigh characters which merely indicate species or species group diversification.

As emphasized throughout the text of this paper, an investigation of the various isolating mechanisms is necessary to assess the morphological characters which are of phylogenetic significance. It has been shown that a classification of the endemic Hawaiian drosophiloids based strictly on external morphological structures can result in a misleading interpretation of evolutionary divergence in the Hawaiian fauna. Spieth (1966, 1968) showed that the striking morphological developments in the males are secondary sexual characters which are utilized in parts of the elaborate, species-specific courtship behavior patterns which apparently play a major role in reproductive isolation between species. However, Throckmorton's (1966) investigation of the internal anatomy, and evidence from the comparison of the male genitalia, show that despite the tremendous morphological diversity displayed by the Hawaiian drosophiloids, they comprise a closely knit group of species which were probably derived from a single ancestral founder. Data from cytological studies also corroborate this hypothesis.

The endemic genera *Antopocerus*, *Ateledrosophila*, *Nudidrosophila* and the species formerly in the genus *Idiomyia* are shown to have male genitalic characteristics (especially in the shape of the aedeagus) which are extremely similar to those of typical *Drosophila* species. The "key" characters used to differentiate these species into separate genera are only secondary sexual characters used by the males in their courtship behavior patterns. The females, however, lack these bizarre structures, and are morphologically typical of the genus *Drosophila*. It is concluded that these so-called "key

characters" of the males are not valid as generic characters and that these four genera are truly cogeneric with the genus *Drosophila*.

It is clear that the Drosophilidae of the Hawaiian Archipelago represent a classical example of explosive evolutionary radiation, and that it presents taxonomists with a group of animals which is speciating at a rate which is enhanced by the diversity of the ecological opportunities existing in the Hawaiian Islands. Taxa at all stages of incipient speciation can be found, and an analysis of the speciation mechanisms is crucial to the understanding of the evolutionary processes which are occurring. In the study of the evolution and genetics of Hawaiian Drosophilidae various basic concepts in the field of systematics and taxonomy are being tested. From the efforts of a team of investigators in various fields of biology, new concepts will undoubtedly be formulated.

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